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FORMULATION OF A PHYLOGENETIC SYSTEM FOR CLASSIFICATION OF VIRUSES

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Since the nature of viruses, their origin and evolution, and the place they occupy in the system of the organic world are among the most important problems of modern biology, it is not surprising that they become the subject of vivid discussions and sharp polemics. Even in the discussion of specific questions of the systematization and nomenclature of individual groups of viruses, it becomes necessary to go beyond the boundaries of subdivisions of virology, because in solving these questions it is impossible to overlook their importance to general biology and to resist expressing opinion on attempts at their solution. Thus it is not surprising that, in an article on the systematization of viruses, Ryzhkov (8) brought up the controversial questions mentioned above, on which no accord has yet been reached in Soviet literature. Much of his article is devoted to an attack on our theories which has continued for many years.

For over 10 years Ryzhkov has given his efforts to questions of the systematization and evolution of viruses (9, 10, 11, 12). It has been a pleasure to observe the evolution of his views on these questions during recent years, an evolution which has led to a retraction of the false concepts he had previously advanced. Although in this article we shall try to justify this statement, we consider our principal task not to attack our critic, but to explain the problem of the nature, origin, evolution, and systematization of viruses.

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In defining viruses as a special category of living beings, attention is usually drawn to their outstanding characteristics, i.e., their small size, their ability to pass through bacterial filters, and the impossibility of cultivating them outside living organisms and tissues. Attention to these characteristics is quite justified, since these properties permit differentiation of viruses from other microorganisms such as bacteria, fungi, and protozoa. However, these descriptive properties, though convenient for the research worker, do not define the essential nature of viruses. Besides, each of these properties, when considered separately, has only a relative importance, because all of them may be discovered in other microorganisms as well.

The largest viruses, i.e., the causal agents of psittacosis and trachoma (not to mention Rickettsia), do not differ in size from "cystocetes" or even from the smallest bacteria. The invisible or filterable forms of numerous bacteria also pass through bacterial filters. Obligatory tissue parasitism is inherent in numerous species of bacteria and protozoa. It is for these reasons that only a combination of the enumerated properties may be used as a criterion for distinguishing viruses from other microorganisms.

All these properties are derivative and based on the essential nature of viruses as noncellular or rather precellular forms of life. The lack of a cellular structure thus becomes the basic property of viruses and differentiates them from other microorganisms such as bacteria, fungi, and protozoa.

Unfortunately, this has not been clearly understood by many authors of works on the nature of viruses. Moreover, certain research workers arbitrarily divide viruses into two groups of a different nature: living matter and living beings. This subdivision is upheld by Moshkovskiy (7), who refuses to apply the concept of species to forms the elementary particles of which cannot be observed by means of a microscope. This viewpoint is shared by Ryzhkov, who in several of his works juxtaposes virus molecules (small viruses) and elementary organisms (large viruses), virus proteins and elementary particles, and virus nucleoproteids and virus liponucleoproteids. Ryzhkov seems unable to foresake this subdivision even in his latest work (8); recognizing viruses as an independent type of organism, he nevertheless subdivides them into crystallobionts and plasmobionts, i.e., two forms which correspond to two different types of the structure of living matter. However, the latest research has established that the same viruses (for instance, influenza virus, bacteriophage) may be either "crystallobionts", or "plasmobionts," depending on circumstances.

A timely remark may be inserted here to indicate the occurrence of filterable forms of numerous bacteria. With every justification these forms may be regarded as lacking cellular structure. For this reason certain authors have identified viruses with other species of microbes (bacteria and fungi). This identification found ardent support in the books and articles written by Bosh'yan (4), Utenkov (13), and Berulava (2). Unfortunately, the theories advanced by these authors are extremely speculative, are unsupported by facts, and cannot be confirmed by control tests and experiments. Although we lack space in this article for a critical evaluation of the work of these authors, let us consider the question of similarity and differences between viruses and filterable types of bacteria. We can agree with Kalina (5) that the filterable forms represent the noncellular stage of the development of bacteria, even though this statement still needs factual confirmation.

However, all similarity between bacteria and viruses ends here, since noncellular forms are merely a definite stage in the development of the bacterial cell, whereas viruses exist only in a noncellular state.

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The problem of the nature of viruses is closely connected with that of their origin. At present, it is doubtful that anyone in our midst adheres to the "theory" of the spontaneous generation of viruses in the tissues of animals and plants as a result of a disorder of metabolism or of the liberation of "genes" from the control of the organism. The prevalent discussions are concerned with other questions: whether viruses are the products of a degenerative development of more highly organized microbes (bacteria, fungi, or protozoa), or whether they should be considered descendants of ancient precellular forms of life.

Bernet (1) is most consistent in defending his theory that viruses are descendants of bacteria, which as a result of a parasitic existence have degenerated by reason of simplification of structure to a transformation into a "bare protein molecule" possessing the elementary properties of life.

O. B. Lepeshinskaya (6) was explicit in her statement that viruses are descendants of ancient precellular forms of life. A similar theory was later adopted by the author of this article.

In this argument Ryzhkov (10) assumed a middle position, which may be best described in his own words: "It may be presumed that, in a world where the largest molecules known to physics and the smallest organisms known to biology are found, there may also be found products of a degradation of life, such as fragments of life and forms of developing life." He retains this position in his latest article, which is now under discussion cf. the following statement: " ... The author always admitted and continues to admit various possibilities as far as the origin of viruses is concerned"), even though he is now more strongly inclined toward the theory that viruses are descended from precellular forms of life.

We believe that Soviet biologists and virologists should assume a clearly defined position on the question of the origin of viruses for the following reasons. First, contrary to Ryzhkov's opinion, much more than "some opinions" and "various assumptions" on the subject are available, namely, concrete facts and data. Second, the problem of the origin of viruses is of great importance to biology at large, and for this reason the battle of opinions on this problem reflects the ideological struggle in biology.

Bernet's hypothesis of "degenerative evolution" (1) is in direct disagreement with facts. If we consider that viruses are products of the degeneration of parasitic bacteria, then the origin of bacteriophages remains unexplained, because a lengthy period of intracellular parasitism is a prerequisite for degenerative evolution. It is unlikely that some bacteria may have lived as parasites in other bacteria. It follows from this theory that there must be a progressive decrease in size and simplification of organization in pathogenic bacteria as compared with related saprophytes. However, the comparison of gonococci to related saprophytic cocci; of the cholera vibrio to para-cholera microorganisms; of the typhoid microbe to B. coli; and comparisons in other analogous pairs indicate that in these instances there is neither change in size nor simplification in the degree of organization.

If the typhoid microbe shows a deficiency of certain enzymes present in B. coli, this is offset by enrichment in antigens such as the Vi-antigens, which are usually absent in B. coli. The same relationships are observed when cholera vibrios and meningococci are compared with related saprophyte species. The loss of some features is offset by the gain of others, this process being caused by the adaptation of microbes to new environments. To postulate a "degenerative evolution" in such cases is to affirm the degeneration of man on the basis of the reduction of the size of the vermiform appendix. On what grounds should we then adhere to these antiscientific concepts which, if logically elaborated, will result in the conclusion that there is transformation of mammals into reptiles, and of palm trees into ferns?

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O. B. Lepeshinskaya (6), who assumed a clearly defined position on this question, was unquestionably right in the following statement: "The metaphysical theories of Virchow no doubt influenced Paul Oduroua in his opinion that viruses originate from those beings most closely related to them, namely the visible microbes. This is an incredible distortion of the theory of evolution. Beyond all doubt, visible microbes represent a more recent development on the phylogenetic scale than the less complicated ultraviruses. Viruses could hardly have originated from visible microbes of recent origin."

We wholeheartedly subscribe to Lepeshinskaya's statement, and consider the question of the origin of viruses to be closely connected with the problem of the origin of life. It is common knowledge that this question is far from being solved at present. This, however, did not prevent Engels, who as far back as the 19th Century exposed the pseudoscientific idealistic theories (for instance, the hypothesis of the drift of embryos from other planets), from outlining the only right path for the solution of this problem, which is based on the methodology of dialectical materialism.

Of course, when we pass on from consideration of the general aspects of the nature and origin of viruses to the particular questions of their evolution, many gaps appear in our knowledge. We are especially ignorant of the early stages of the evolution of viruses, and this is essential information for the construction of a phylogenetic systematization of viruses.

To assume that we have no knowledge at all in this field would be an error. The data accumulated so far can serve as a basis for formulating working hypotheses which will induce active and practical determination and assimilation of new data essential for solving the problem. This more active attitude ought to replace the passive, patient waiting for further developments.

Let us consider certain facts which may shed some light on the early stages of the evolution of viruses. As previously indicated, all viruses known at present lack cellular structure, and all of them are intracellular or tissue parasites. Although they possess these common properties, viruses differ so sharply in the construction of their particles that considerable confusion arose among scientific workers and still prevails. Some scientists firmly refused to incorporate them into one type (Moshkovskiy /7/, Troll /15/). Others did so with a great deal of reservation (Ryzhkov). We assume, on the other hand, that the differences demonstrate something entirely different: the extreme length of time during which the parasitism of viruses existed. As a result of the length of the time involved, various groups underwent a long process of evolution linked with the evolution of their hosts. This evolution resulted in modern viruses, which are so sharply different in their forms.

Viruses are widespread in modern lower plants (bacteria and actinomycetes). A virus disease has been discovered in lower animals (infusoria). The existence of viruses affecting one-celled plants and animals also supports the assumption that development of parasitism in viruses is ancient. A comparison of viruses of bacteria (bacteriophages) and protozoa viruses (cappa factors) indicates the presence of essential differences expressed to no lesser extent than in various classes of animals and plants.

We may thus assume that the distinctions between modern viruses and their ancestors follow the pattern of distinctions between primary unicellular animals and modern infusoria or between primary unicellular plants and modern bacteria. We have been told that these conclusions are not validated by facts because, although a large number of phages has been discovered, only one virus of protozoa is known. However, at one time, all

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discussions and assumptions about the phylogenesis of chordates were based on the study of only one lancelet. Of great interest for understanding the possible ways of evolution is the study of diseases of the smallpox group. Diseases of this type have been observed in mammals, birds, and fish, and the causal agents of these diseases bear a remarkable resemblance in size, morphology, and chemical composition; but we can hardly speak of an adaptation to birds or mammals of the virus of smallpox of carps.

The assumption of an evolution of this group of viruses that was linked to the evolution of their hosts from fish to mammals seems much closer to the truth. Interspecies transitions [of viruses] among domestic animals may have occurred in recent times. We must admit that we do not know of any analogous viruses in amphibians and reptiles. However, in the first place, no one has searched for such viruses, and, in the second place, there are hardly any grounds for affirming that all intermediate forms should have been preserved to the present, in view of the fact that the reptilian age was followed by mass extinction of these species. A similar situation is observed with regard to viruses producing tumors found in fish, amphibians, and mammals. These viruses show a highly specialized form of adaptation and resemble each other closely in size, morphology, and chemical composition. A transition to other species of hosts is even less possible for them. It is very likely that this group of viruses went through a long-term process of evolution linked with the evolution of their hosts from fish to mammals.

Through lack of space, we shall limit our discussion to data pertinent to conclusions about the ancient origin of viruses, their descent from primary precellular forms of life, the ancient origin of the parasitic type of existence of viruses, and the long-term evolution of certain types of viruses in conjunction with the evolution of their hosts. It was on the basis of these data and conclusions from them that we made the assumption that viruses are descended from primary precellular forms of life and that they became adapted to parasitism before the division of the organic world into the animal and vegetable kingdoms. In the course of a further evolution of the organic world, there appeared large and sharply defined groups of viruses, such as bacteriophages, viruses of higher plants, and viruses of animals, which in our systematization have been incorporated into separate groups.

Let us consider in detail the early stages of the evolution of viruses. In the course of the evolution of the organic world and of its development toward increased complexity of biocoenotic relationships, increasingly wider scopes were opened for an interspecies exchange of viruses, not limited to the framework of just one kingdom, but including species of both the animal and vegetable kingdoms. Of course, a narrow range of specialization, such as that described above in the case of viruses of smallpox and tumors, creates certain obstacles to this exchange. Nevertheless, these obstacles can be overcome, as demonstrated in the case of rickettsiae. That rickettsiae were originally parasites of arthropods, and that their evolution for a long time was confined to this class, can now be accepted as a proven fact. With the transition of some arthropods to bloodsucking, new possibilities were opened for the evolution of rickettsiae.

The transport of rickettsiae into the blood of mammals (and perhaps birds) caused conditions favorable to a wider propagation of these microorganisms: they found good nutrition in the tissues of warm-blooded animals, and these animals could easily contaminate a large number of arthropods. Instead of being transmitted by the transovarian path and perhaps by sexual contact of arthropods, rickettsiae are now being transmitted in a new way, with an alternation of two hosts - an arthropod and a warm-blooded animal. This process involves new species of arthropods (cf. tick rickettsiosis, flea rickettsiosis, and lice rickettsiosis). A change in the character of relations

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between the rickettsiae and their hosts takes place: an acute rickettsiosis infection of warm-blooded animals replaces the symbiosis of rickettsiae and arthropods.

The polyhedral diseases of insects may possibly serve as examples of the intraspecies transition of viruses between different kingdoms. The morphology and chemical composition of these viruses suggest to some extent that they are closer to the primary viruses of plants than those of animals. A characteristic of this group of viruses, which can hardly be called accidental, is that they affect only the larvae of insects (i.e., caterpillars) that freely consume the leaves of higher plants which in turn are frequently stricken by morphologically similar viruses. Consequently, the assumption that this group of viruses is derived as a result of the adaptation of plant viruses to insects, followed by a break with their former hosts, may not be entirely groundless. Further research will indicate the truth or falsity of this assumption. It also may be possible that numerous viruses which affect plants and are transmitted exclusively by insects are examples of a similar, but uncompleted process of adaptation of plant viruses to the organisms of insects. However, a reverse process is also possible, i.e., an adaptation of an insect virus to the organism of plants.

We could continue the enumeration of similar examples and draw an analogy between the bacteriophage-multiplication cycle and that of the influenza virus, attempting to establish possible genetic ties between these viruses. We could also make a comparison between rickettsiae and large viruses, e.g., the causative factor of psittacosis. However, it seems hardly worth while, especially since enough analogies and similar arguments have been presented by Ryzhkov in his article.

As for the fact, noted by Ryzhkov, of the disproportionate distribution of viruses among the various groups of the animal and vegetable kingdoms, we do not consider this distribution unusual. On the contrary, it seems quite natural since it demonstrates the uneven application of virological study to various systematic groups and also reflects the biocoenotic ties which exist at present between various species. The list of /known/ viruses that affect various systematic groups of the organic world will doubtlessly increase. Only recently we believed that moss was free of virus diseases, but the research of Blattni (3) and his associates demonstrated the presence of virus diseases in three species of moss. We may be sure that soon there will be discoveries of virus diseases in many animals and plants previously considered free of this type of disease. It is also quite clear that the process of the exchange of viruses between various groups of the organic world is uneven. The mere fact that bloodsucking arthropods parasitize mostly mammals and birds rather than fish and amphibians cannot be overlooked as a cause of the abundance of correlated viruses in the first group and of their absence in the second.

The numerous viruses now existing are products of a lengthy evolution of the organic world. Many viruses, formerly active, have become extinct together with their hosts. Some have survived, but in a somewhat altered form, while the majority emerged within a recent period and are continuing to emerge. The relative simplicity of the organization of viruses and the rapidity of their propagation explain the fact that species formation in the world of viruses takes place faster and runs a more intensive course than in the case of highly organized animals and plants. It is this which makes the work of tracing the evolution of viruses so difficult. We attempted to formulate a theory of this evolution on the basis of data accumulated to date, though we are fully aware that any new discoveries may call for a revision of the working hypotheses here advanced.

The above analysis clearly demonstrates the error of Ryzhkov, who accuses us of substituting "discussion unsupported by arguments" for the work of phylogeneticists. He is only wasting his time in attempting, by means

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of naive analogies, to refute the classification of viruses according to their habitat in conformity with a theory which he wrongly attributes to us. Actually we set up three principal classes of viruses, not according to their habitat, but on the basis of phylogenetic considerations stemming from considerable factual data amassed by virology. Besides all the data submitted above, which support the phylogenetic theory we advocate, the sharp delineation of the virus classes mentioned above further supports our statements. All thoroughly investigated bacteriophages have a spherical shape (frequently with a tail), a similar chemical composition (they contain thymonucleic acid), and a characteristic cycle of development in the organism of their host. The metabolism processes of all well-known phages are similar; all of them parasitize in the organisms of bacteria and actinomycetes. We advocate classification of this group as an independent class, while Ryzhkov considers this classification antiscientific but still classifies bacteriophages as an independent class.

The best-known viruses affecting higher plants have a threadlike or globular shape and a similar chemical composition (they contain yeast nucleic acid). One of their characteristic properties is their ability to form crystal-like structures. They infect higher plants, and are transmitted through the sap and through the agency of arthropods. We classify this group of viruses as a separate class. Ryzhkov considers this classification antiscientific but still classifies these viruses as an individual class.

Let us now consider the further coincidences occurring in the two systems being compared: the order of Polyhedrales which we set up corresponds in Ryzhkov's system to the class of Pseudocrystallinae consisting of a single order. The three orders amalgamated by Ryzhkov into the class of Chlamydozoa correspond almost exactly in their species composition to the orders of Rickettsiales, Strongyloplasmales, and Gamaleiales proposed by us. However, in the first order we included Rickettsiales as well as Chlamidozoa. Finally, the viruses of animals, included in the class of Arthropodophilae by Ryzhkov, are completely covered by our order of Arthropodophiliales. It seems that if such classification is unscientific, this term should apply to both systems under consideration.

Let us now consider the differences between our system and Ryzhkov's. Among the viruses affecting plants, there is a large group on the morphology and chemical composition of which we have no information. We know only that they are transmitted by insects, in the organism of which they undergo a definite stage of development. Bearing in mind that it is far better to "clearly formulate the specific aspects about which we lack the knowledge than to attempt to cover the situation by rash expressions of opinion," and considering "that a classification of viruses in accordance with their habitat rather than according to their properties is unscientific," considered it impossible to amalgamate these plant viruses into the same group with transmissible viruses of warm-blooded animals, the properties of which are well known, and which form a clearly differentiated group.

To our surprise, Ryzhkov amalgamated all these different viruses into one class, classifying them according to their habitat (the organism of arthropods). This is a method which he had previously condemned. Concerning our unification into one class of viruses seemingly as different as the representatives of the orders Protovirales (poliomyelitis), Arthropodophiliales (tick encephalitis), Gamaleiales (influenza), Strongyloplasmales (smallpox), and Rickettsiales (psittacosis), we based our classification on the similarity of biological properties, which was demonstrated to a greater extent between these groups of viruses than, for instance, between bacteriophages and mosaic disease viruses. A comparison of the transmissible poliomyelitis virus of Mengo with the causative factor of Scotch encephalitis will disclose more common traits than a comparison of the Mengo virus with tobacco mosaic virus. It hardly would be permissible to join into one family such different entities as the virus of tomato bushing and the causal agent of hoof-and-mouth disease.

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In conclusion, we shall compare the approaches of our system and Ryzhkov's system to the classification of minor systematic groups.

Ryzhkov's System

Class: Arthropodophilae

Order 1. Pantropiales

Family 1. Pantropiaceae

Genera: 1. Pontropus (Crimean and Omsk hemorrhagic fevers, Colorado tick fever, and Singo fever)

2. Aedephilus (dengue, pappataccі fever, and yellow fever)

Order 2. Neurotropiales

Family 1. Neutrotropiaecae

Genera: 1. Neurotropus (American equine encephalitis)

2. Encephalotropus (tick encephalites, louping-ill, mosquito encephalites, and keratoconjunctivitis)

Order 3. Leptomotropiales

Zhdanov's System

Order: Arthropodophiliales

Family 1. Acarophilaceae

Genera: 1. Encephalophilus (tick encephalitis, louping-ill, and certain types of mouse encephalomyelitis)

2. Meningophilus (choriomeningitis and chorioencephalitis)

3. Haemorrhagogenes (hemorrhagic fevers)

Family 2. Insectophilaceae

Genera: 1. Insectophilus (yellow fever, dengue, mosquito encephalites, keratoconjunctivitis, and certain mosquito viruses)

2. Febrigenes (pappataccі and other fevers)

Family 3. Polyvectaceae

Genus: Polyvectus (American equine encephalitis, encephalomyelitis, and Colorado fever)

Ryzhkov based the systematization of the first two orders on such precarious criteria as the clinical aspects of animal diseases caused by viruses. That this method, applied previously by Holmes (14), leads to incongruous results, is a well-known fact. This is apparent from the following example. Comparative research has established the presence of antigenic similarity between the causal agents of tick encephalitis and of hemorrhagic fevers. Recent work has demonstrated that certain viruses of spontaneous encephalomyelites of mice have common antigens with the viruses of encephalitis and of choriomenengitis (the so-called intermediate strains). Further research has also established the existence of genetic connections between the viruses of yellow fever, dengue, and certain mosquito viruses found in natural foci of yellow fever. The ecological similarity of these viruses was already known. It also was found that the virus of yellow fever is immunologically very close to a group of related viruses, i.e., the causal agents of mosquito encephalites (Japanese, St Louis, West Nile, and Ilheus) and of epidemic keratoconjunctivitis. Thus, the existence of a sharply defined group of viruses transmitted by mosquitoes and causing fevers and encephalitis was established. The group of causative factors of American equine encephalomyelitis stands apart.

It was on these proven facts, established and tested by research and experimentation, that we built the systematization of transmissible viruses described above. We have grounds to hope that the systematization of this

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group of viruses is a natural and a close approach to phylogenetic systematization. Moreover, the example cited above is a good illustration of the unfitness of the use of clinical symptomatology for setting up even the smallest systematic groups (for instance, the order of Insectophilus includes the causal agents of yellow fever, Japanese encephalitis, and epidemic keratoconjunctivitis, which are immunologically very closely related and doubtless have common roots of origin), not to mention such large groups as orders and families.

It is difficult to present briefly all the numerous questions about the problems of the nature of viruses, their origin, evolution, systematization, and nomenclature. We have attempted to show that the factual data accumulated in the course of the development of virology have already allowed us to approach the solution of some of these questions on scientifically proven grounds. We have also attempted to indicate certain ways for solving these questions. The battle of opinions and a critical discussion of this problem will undoubtedly assist the successful development of Soviet virology, which is ready and able to solve large-scale problems of general biological significance.

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